

Rapid warming induces the contrasting growth of Yezo spruce (*Picea jezoensis* var. *microsperma*) at two elevation gradient sites of northeast China

Liangjun Zhu^{a,b}, David J. Cooper^b, Jingwen Yang^a, Xu Zhang^a, Xiaochun Wang^{a,*}

^a Center for Ecological Research, School of Forestry, Northeast Forestry University, Harbin, 150040, China

^b Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, 80523, USA

ARTICLE INFO

Keywords:

Growth decline
Basal area increment
Elevation gradient
Drought
Dendrochronology
Climate change

ABSTRACT

Accurately assessing the impact of climate changes on tree growth or forest productivity is vital to better understand global carbon cycles. Here, we carried out dendroclimatological research on Yezo spruce (*Picea jezoensis* var. *microsperma*) along an elevation gradient in two sites to investigate the effect of rapid warming on spruce growth in northeast China. Results indicated that trees at two low-elevation sites had significantly wider ring widths and higher basal area increment (BAI) compared with high-elevation sites. Ring widths and BAI of Yezo spruce at low elevations showed a clear growth increase during the 1940s–1970s followed by a significant decline after 1980. However, trees at high elevations showed a relatively stable growth during the 1940s–1970s followed by a significant increase after 1980. Rapid warming after 1980 increased the radial growth of Yezo spruce at high-elevation sites, but reduced tree growth at low-elevation sites. Winter precipitation and growing season temperature were positively correlated with radial growth of Yezo spruce at high elevations, but negatively correlated with tree growth at low elevations. A clear pattern of growth and growth-climate relationship changed in 1980. The temperature threshold for determining the impact of climate on Yezo spruce could change with latitude or site. Difference in drought caused by warming may be the main reason for the opposite response of tree growing at different altitudes in northeast China. The mechanism of rapid warming driving contrasting growth at different elevations should also be investigated in other tree species in NE Asia. In the context of future climate warming, our findings are of great significance for tree growth in assessing forest dynamics and carbon cycling.

1. Introduction

Climate warming is an important driver of global change that can affect the distribution, growth and reproduction of plants that control the absorption and emission of carbon dioxide and influence global carbon cycle pattern (IPCC, 2013). Over the past 150 years a significant warming has occurred at high latitudes of the Northern Hemisphere, most prominently after the 1980s (Consortium, 2013). In many areas a decrease in precipitation also occurred resulting in drought conditions (Dai, 2013). During the past several decades most forests have undergone distinct changes in species composition and distribution, tree regeneration, growth and death, forest ecosystem structure and function, and forest productivity that are linked to warming (IPCC, 2013; Camarero et al., 2015; Jørgen et al., 2015). It is important to understand the relationship between climate variation and forest vegetation to assess the impacts of climate change on forest ecosystems. This could allow us to predict future changes in forest vegetation and adapt forest management practices and strategies to more adequately ensure the

sustainable functioning and use of forest ecosystems (Barber et al., 2000; Jump et al., 2006; Salzer et al., 2009; Sidor et al., 2015).

Radial growth or productivity of trees is one of the most direct, sensitive, and easily measured indicators of forest dynamics, and is widely used for assessing the effects of climate change on trees (Jump et al., 2006; Salzer et al., 2009; Sidor et al., 2015). Tree and forest declines due to high temperatures inducing severe drought conditions have been documented in many regions (Barber et al., 2000; Jump et al., 2006; Liu et al., 2013). However, other studies suggest that rapid climate warming has increased tree growth and forest productivity (Gou et al., 2007; Salzer et al., 2009; Jørgen et al., 2015; Zhu et al., 2015a). Many biotic and abiotic factors make it difficult to understand the interactions between forest ecosystems and climate, but environmental variance along an elevation gradient might be an important factor affecting tree growth (Yu et al., 2006; Babst et al., 2013; Yao, 2013; Pellizzari et al., 2014; Sidor et al., 2015; Wang, 2015).

Yezo spruce (*Picea jezoensis* var. *microsperma*) is an important evergreen coniferous tree native to NE Asia and can grow 30–50 m tall

* Corresponding author.

E-mail address: wangx@nefu.edu.cn (X. Wang).

with a trunk up to 2 m in diameter. It ranges from central Japan and North Korea, to the maritime provinces of NE China, and extending north into the Russian far east (Thomas et al., 2013). It occurs from near sea level to 2700 m above sea level (a.s.l.), and has good yield and high-quality performance in many soil types and site conditions, producing high-quality timber. In several forests types, it is a co-dominant and is commonly harvested with other conifers or broadleaf trees, such as *Pinus koraiensis* Sieb. et Zucc., *Betula costata* Trautv., *Larix gmelinii* Rupr., *Fraxinus mandshurica* Rupr. and *Abies nephrolepis* Maxim. In recent decades excessive logging in many parts of its range has sharply reduced the population of Yezo spruce, especially when clear cutting is followed by repeated burning that limits its regeneration (Thomas et al., 2013). The decline of Yezo spruce may seriously threaten the economic and ecological security of NE Asia. Some protection and restoration of Yezo spruce has begun in parts of NE Asia to protect its high economic and ecological value. For instance, the Chinese government has invested each year in the restoration of spruce forest. Unfortunately, afforestation has been unsuccessful and unsatisfactory due to low sapling survival and slow growth rates.

Yu et al. (2006) pointed out that rapid warming during the past 20 years did not influence radial growth of Yezo spruce along an elevation gradient in the Changbai Mountains, northeast China, because annual total precipitation declined during the same period. In recent years, Li et al. (2011) reported a declining growth trend related to climate warming at the upper elevational limits of Yezo spruce in the Changbai Mountains. However, Wang (2015) clarified that radial growth of Yezo spruce has a declining growth trend at 1000 m a.s.l. and a relatively stable or slightly upward growth trend at higher (1300 m and 1750 m a.s.l.) elevations. Hence, larger scale analyses are needed to clarify the growth patterns and evaluate the effect of climate change on Yezo spruce. We carried out a dendroclimatological analysis of the radial growth of Yezo spruce along an elevation gradient covering its natural altitudinal range in the Laobai and Xiaoxing'an Mountains, NE China. Our aims are: (i) to investigate the main climate factors limiting the radial growth of Yezo spruce, (ii) to reveal the difference in growth patterns and growth-climate responses of Yezo spruce along an elevation gradient and, (iii) to highlight the different effects of rapid warming (after 1980) on radial growth and dendroclimatic relationships of Yezo spruce at different elevations.

2. Materials and methods

2.1. Study area and climate

Yezo spruce is a long-lived, shallow-rooted, shade-tolerant species, occurring from 300 to 1800 m a.s.l. in NE China. Across its range (40.75–49.82°N, 124.75–135°E, Fig. 1), two representative sampling areas along an elevation gradient were selected in the Laobai Mountains (1692 m a.s.l.; hereafter LM) and Xiaoxing'an Mountains (1429 m a.s.l.; hereafter XM). The Yezo spruce community occupies an elevation range from approximately 800 to 1550 m and 300 to 1429 m a.s.l. in the LM and XM areas.

Our study area is a typical temperate continental monsoon climate, characterized by long cold winters and short cool rainy summers. Annual mean temperature is 1.8 °C and 3.2 °C at XM and LM, and annual total precipitation is 636 mm and 623 mm (Table 1). January and July are the coldest and warmest months and more than 80% of annual precipitation are received from May to September (Fig. 2). The soils in the study area are classified as Haplumbrepts or Eutroboralfs (dark-brown forest soil in Chinese soil taxonomic system) (Li 1997). Soil depth becomes shallower with increasing elevation and slope. Soil in valleys or flats at low elevations is approximately 50 cm deep or more, while in the steep slopes or high elevation areas the soil is only 20–30 cm deep. The distinct precipitation and temperature gradient and varied topography strongly influence local or regional vegetation composition. Forest vegetation in the study area varies from coniferous

and broad-leaved mixed forests at lower elevation (300–1100 m a.s.l.) to subalpine coniferous forest at higher elevation (1100–1600 m a.s.l.). The forests are often composed of *Picea koraiensis*, *Abies nephrolepis*, *Betula ermanii* or *Pinus pumila* at high elevation, and *Picea koraiensis*, *Pinus koraiensis*, *Abies nephrolepis*, *Abies holophylla*, *Acer mono*, *Tilia amurensis*, *Tilia mandshurica*, *Betula costata* and *Betula platyphylla* at low elevation.

2.2. Core sampling and chronology development

We identified five elevations along Yezo spruce's elevation range (350, 610, 920, 1250 and 1430 m) in the XM region and three elevations (900, 1200 and 1500 m) in the LM region for coring trees (Table 2). Each site is named as its location and elevation, for example sampling site X350 is at elevation of 350 m in the XM region. The X350 site (in Liangshui; 47°11'N, 128°54'E) is about 60 km from the X610, X920, X1250 and X1430 sites (in Taoshan). At each site, we chose mature stands without recent history of natural and anthropogenic disturbance and collected at least 25 cores from living and undamaged Yezo spruce during spring 2016. All trees were taken one or two cores at ca. 1.2 m height with a 5.15-mm increment borer (Mora, Sweden). Information of the latitude, longitude, slope, and vegetation of the sampling site is shown in Table 2.

In the lab, all cores were mounted, air-dried and progressively sanded until tree rings were clearly visible. Then, rings were visually cross-dated under a microscope using the skeleton-plot method (Stokes and Smiley, 1968) and ring widths were measured with a precision of 0.001 mm using a Velmex tree-ring system (Velmex, Inc., Bloomfield, NY, USA). The quality of dating and measurement was checked using the COFECHA program (Holmes, 1983). We used a conservative standardization method, viz. fitting a negative exponential curve or a regression line, to remove age-related trends (Cook, 1985). Standardization was performed with the ARSTAN program (Cook, 1985), and the standard chronologies (STD) were used for further analyses. The statistical characteristics of each chronology and their correlation matrix during the period 1900–2015 are shown in Tables 3 and S1.

2.3. Basal area increment (BAI) measurements

We can not confirm whether growth decline occurs only through the width of annual rings because the ring widths typically decline with the increase of trees age and/or diameter (Phipps and John, 1998). Basal area increment (BAI), typically has a brief period of early growth suppression (suppression phase) followed by a rapid increase (release phase) in annual basal area growth. Unlike width, BAI in healthy mature trees may continue to increase or stabilize through time, and does not have a decreasing trend until a tree senesces (Jump et al., 2006). Therefore, a decline in tree growth could be strongly indicated by a negative trend in BAI. The BAI was calculated using the following equation:

$$BAI = \pi(R_n^2 - R_{n-1}^2), \quad (1)$$

where R is the tree radius and n is the year of ring formation. In this study, BAI of each tree/core was computed by the Program Biaplt_xp (<http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software>). In the case of cores that did not hit the pith, we estimated the number of years missing to pith by fitting a geometric pith locator to the innermost rings which considered the mean growth rate and radian/angle of the missing parts of the radius (Camarero et al., 2015). The mean BAI values at each site were calculated by averaging all BAI series.

2.4. Climatic data and statistical analysis

Historical climate data from the nearest Tieli and Dunhua weather

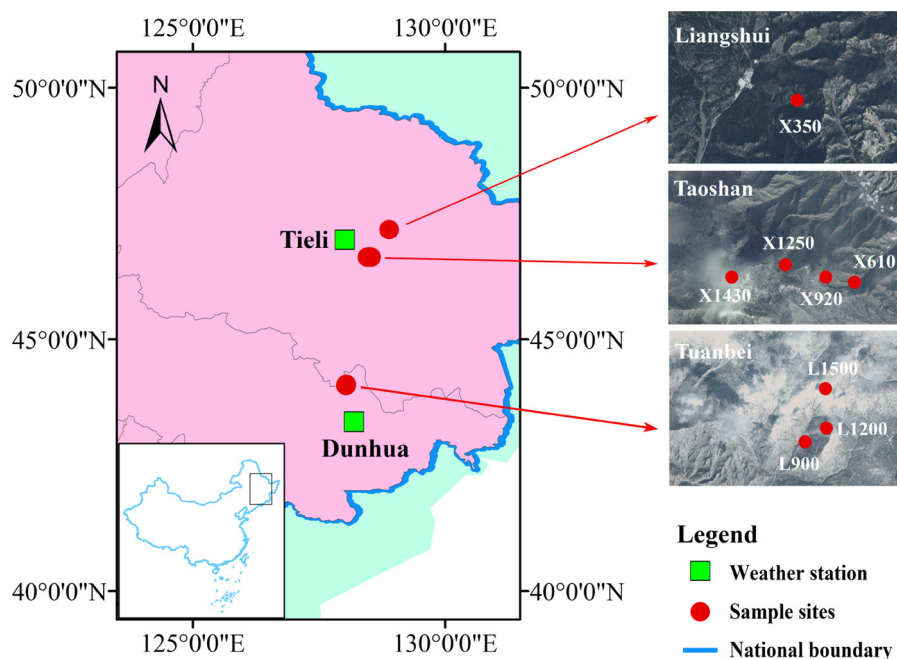


Fig. 1. The distribution of sampling sites (red circles) and weather station (green squares). The sampling site code is the same as in Table 2 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

stations were obtained from the China Meteorological Data Service Center (<http://data.cma.cn>; Table 1 and Fig. 1). Regional climate was calculated by averaging climate variables from the two weather stations. Linear regressions of temperature and precipitation for both weather stations were performed for three sequential periods (pre-1979, 1980–1998 and 1999–2015). The years of 1980 and 1998 are important break points in climate record that are widely used in this research. The slope and coefficient of determination of linear models were used to evaluate the fitness and rates of climate change. Climate variables including monthly total precipitation, mean, minimum and maximum temperature (Fig. 2) were used for growth-climate response analysis. Correlation analysis between tree-ring chronologies and climatic data was undertaken using an 18-month window from the previous May (hereafter, P5) to the current October (hereafter, C10).

Cluster analysis was performed to identify groups of trees with similar growth patterns. Correlation coefficients between tree-ring index (TRI) and monthly precipitation and mean temperature from the statistically independent characteristics P5 to C10, were chosen as input data to create the Pearson distance matrix. According to the results of cluster analysis, those chronologies with similar characteristics were averaged as regional chronologies (Fig. 3). Pearson correlations between regional chronologies and regional climate from P5 to C10 were calculated to explore tree growth-climate relationship.

We carried out a moving 20-yr window correlation analyses using DENDROCLIM2002 to analyze the temporal stability of dendroclimatic relations (Biondi and Waikul, 2004). Linear regression was used to identify temporal trends of BAI at each site for the two periods before and after 1980. The climatic and BAI data at different periods or sites were compared by using a *t*-test or multiple comparisons. Regression

analysis was conducted using SigmaPlot 12.5 (Systat Software, Inc., Chicago, IL, USA). All other statistical tests were performed using the SPSS 19.0 software package (IBM SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Climate trends in recent decades

Annual precipitation was different in recent decades from the full record. Mean annual total precipitation in Tieli (636 mm) was similar to Dunhua (623 mm) and the monthly distribution of annual precipitation was also similar (Table 1, Fig. 2). However, annual precipitation at both sites significantly ($p < 0.01$) declined from 1950 to 1980, with a slope of -9.77 and -6.58 mm year $^{-1}$, respectively (Fig. 4). After 1980, a drying trend is recorded at the Dunhua weather station, although it was not statistically significant. At the Tieli weather station, a wetting trend occurred during the period 1999–2015. A significant ($p < 0.01$) wetting trend of 19.84 mm year $^{-1}$ and a non-significant drying trend after 1998 in Tieli and Dunhua weather stations (Fig. 4) was the main difference in precipitation.

Annual mean temperature in Dunhua (3.2 °C) was nearly double that of Tieli (1.8 °C) (Table 1). A warming trend in recent decades was observed across the study area (Fig. 4). A *t*-test revealed a highly significant difference in annual mean temperature from a mean of 1.1 °C during 1958–1980 to 2.3 °C during 1999–2015 in Tieli ($t = -5.88$, $p < 0.0001$) and from a mean of 2.7 °C during 1953–1980 to 4.1 °C during 1999–2015 in Dunhua ($t = -7.9$, $p < 0.0001$). Both Tieli and Dunhua had a significant ($r = 0.64$ and $r = 0.75$, $p < 0.01$) warming trend with a rapid increase of 0.90 °C and 0.99 °C per decade (Fig. 4).

Table 1

Information of the climate stations affiliated with each site.

Climate station	Sites	Lat. (°N)	Long. (°E)	Elev. (m)	MAT (°C)	TAP (mm)	DWS (km)	Time span
Tieli	XM	46°59′	128°01′	211	1.8	636	43/69	1958–2015
Dunhua	LM	43°22′	128°12′	525	3.2	623	70	1953–2015

Note: MAT-mean annual temperature, TAP-total annual precipitation. DWS-the distances from each weather station to its respective sampling site.

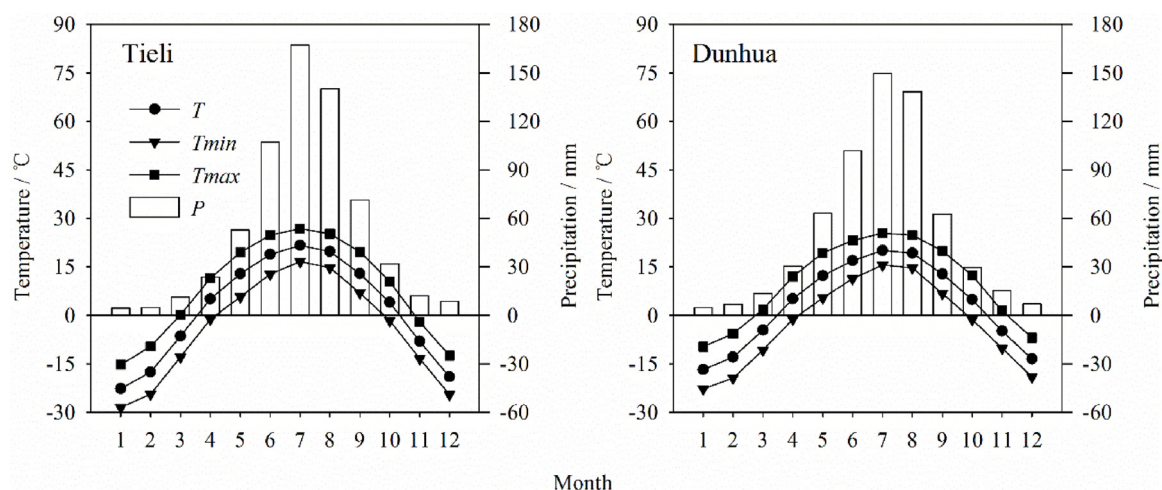


Fig. 2. Monthly sum of precipitation (P) and mean (T), minimum (T_{min}) and Maximum (T_{max}) temperature of Tieli and Dunhua meteorological stations.

Table 2

Location of Yezo spruce sampling sites and sites descriptions.

Region	Site	ID	Lat. (°N)	Long. (°E)	Elev. (m)	Aspect	Slope (°)
XM	Liangshui	X350	47°11'	128°54'	349	North	5–15
	Taoshan	X 610	46°38'	128°32'	611	North	30–45
	Taoshan	X 920	46°38'	128°31'	917	North	< 10
	Taoshan	X1250	46°38'	128°30'	1245	West	< 10
	Taoshan	X1430	46°38'	128°28'	1429	Northeast	< 5
LM	Tuanbei	L900	44°05'	128°02'	908	South	< 5
	Tuanbei	L1200	44°06'	128°03'	1194	South	45–65
	Tuanbei	L1500	44°06'	128°03'	1506	South	45–55

Note: XM, Xiaoxing'an Mts.; LM, Laobai Mts.

Overall, the 1980s were cold and wet, and appeared as an inflection point from a climatic point of view. Since then, warmer and drier conditions have begun to prevail in the study area.

3.2. Elevation-related ring-width & BAI trend

Tree-ring widths in the XM region decreased with the increase of elevation (except sites X920 and X1430). Ring widths at X350 and X920 had an increasing trend during the 1940s–1970s followed by a declining trend until present (Fig. 5). Trees at sites X610, X1250 and X1430 showed a significant increasing growth trend until the end of 1970s, especially at X1250 with widths up to 4 mm per year in the most recent ten years (Fig. 5). Microhabitat differences, such as the area at X1430 (heavy snowpack) or soil types (X920), might influence tree growth abnormalities (Table 2). Tree growth at X920, caused by the poor rock dominated soil, was similar to those at low-elevation valleys and is treated as a low elevation site.

In the LM region, the variation of Yezo spruce growth at 1200 and

1500 m a.s.l. (high elevation sites) was small (SD: 0.2 and 0.17), with an averaging grow rate of 0.87 mm to 1 mm per year, whereas trees growing at lower elevation (900 m a.s.l.) showed a large variation of growth pattern with a higher growth rate (Fig. 5). Like the XM region, the mean growth rate at L900 showed a significant increasing trend from the 1940s to 1970s when the fastest growth rate exceeded 3 mm per year, then a rapid decline from the 1980s to present (Fig. 5). Overall, a comparison of ring widths showed that trees at lower elevations grew considerably better over their lifespan than trees at higher elevations (Fig. 5).

Overall, trees growing at low elevations, such as at X350 and L900, showed a higher BAI than trees at higher elevation (Table 4). At low elevation, all tree groups exhibited a clear increase in productivity from the 1940s–1970s followed by a decrease in BAI until present. BAI of trees at high elevation showed an increasing trend since 1980 (Table 4). At all sites except L1200, mean BAI during 1981–2014 was remarkably higher than the BAI during the period 1947–1980. During 1947–1980, the BAI increased at all sites except X1250, and the rate of growth

Table 3

Site description and statistical characteristics of the *Picea jezoensis* chronologies used in this study.

Site code	MRW (mm)	Age \pm SD	Time span	SNR	MS	AC1	EPS	RBAR	No. T/C
X350	2.08	109 \pm 35	1851–2015	11.2	0.16	0.86	0.92	0.50	35/35
X 610	1.40	87 \pm 34	1878–2015	9.0	0.18	0.94	0.90	0.46	22/30
X 920	1.44	103 \pm 37	1817–2015	12.7	0.15	0.81	0.93	0.49	55/78
X1250	1.39	76 \pm 30	1868–2015	16.3	0.18	0.92	0.99	0.53	38/65
X1430	1.35	81 \pm 24	1888–2015	15.7	0.15	0.73	0.94	0.58	27/56
L900	1.48	135 \pm 37	1802–2015	14.6	0.19	0.95	0.94	0.50	64/64
L1200	0.76	255 \pm 62	1672–2015	7.5	0.17	0.76	0.88	0.58	27/27
L1500	1.04	183 \pm 46	1760–2015	7.1	0.15	0.55	0.88	0.59	35/35

Note: MRW-mean ring width, SNR-signal-noise ratio, MS-mean sensitivity, AC1-first-order autocorrelation, EPS-expressed population signal, RBAR-mean interseries correlation, No. T/C-tree/core numbers.

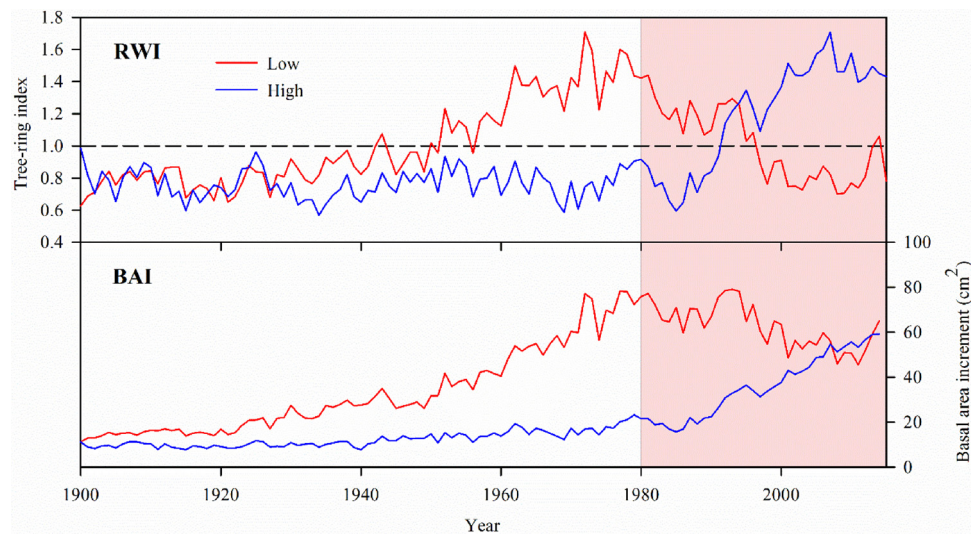


Fig. 3. Temporal variation of regional averaged tree-ring index and BAI at low and high elevations.

increase at X350 site reached $0.63 \text{ cm}^2 \text{ year}^{-1}$ ($p < 0.0001$, Fig. 5 and Table 4). After 1980, trees at X1250 showed the highest increasing rate of BAI ($0.75 \text{ cm}^2 \text{ year}^{-1}$, $p < 0.0001$, Fig. 5 and Table 4), while those at L900 showed the lowest rate of BAI change ($-0.43 \text{ cm}^2 \text{ year}^{-1}$, $p < 0.0001$, Fig. 5 and Table 4). Linear regression indicated that a negative rate of BAI occurred at X350, X920, L900 and L1500 sites after 1980, which confirmed that a similar decline trend of Yezo spruce growth occurred at low elevations (Table 4).

3.3. Regional chronology and its relationship with climate

Pearson correlations indicated that temperature had a negative effect on TRI of Yezo spruce at low-elevation sites (X350, X920, L900 and L1200) and a positive effect at high-elevation sites (X610, X1250, X1430 and L1500) (Fig. S1). The effects of winter precipitation on tree growth were opposite, being negative at low and positive at high-elevation sites (Fig. S2). Cluster analysis further confirmed that the L900, L1200, X350 and X920 sites belonged to a group of low elevation sites,

and the others sites belonged to a group of high elevation sites (Fig. 6), which were consistent with the results of the BAI trend analysis (Fig. 3).

Correlations coefficients between the regional chronologies and climate revealed an opposite pattern of tree growth-climate relationship between low and high elevation sites (Fig. 7). Winter precipitation had a positive effect on trees growing at low elevations ($r_{P12} = 0.29$ and $r_{C3} = 0.38$, $p < 0.05$) and a negative effect on trees at high elevations ($r_{C1} = -0.32$ and $r_{C3} = -0.42$, $p < 0.05$). Although the effect of summer precipitation on tree growth was not significant, it also showed an opposite effect on tree growth at low and high elevations. Like precipitation, this opposite tree growth-climate relationship between low- and high-elevation sites also occurred at temperature, especially at mean and maximum temperature. A significant negative relationship between mean temperature and TRI at low elevations was found on months P5-P11, C1-C2 and C4-C10, whereas a significantly positive effect on tree growth at high elevations were found on months P5-P11, C2 and C5-C10 (Fig. 7). Minimum temperature for all months except P11 showed a negative effect on tree growth at low-elevation sites. On

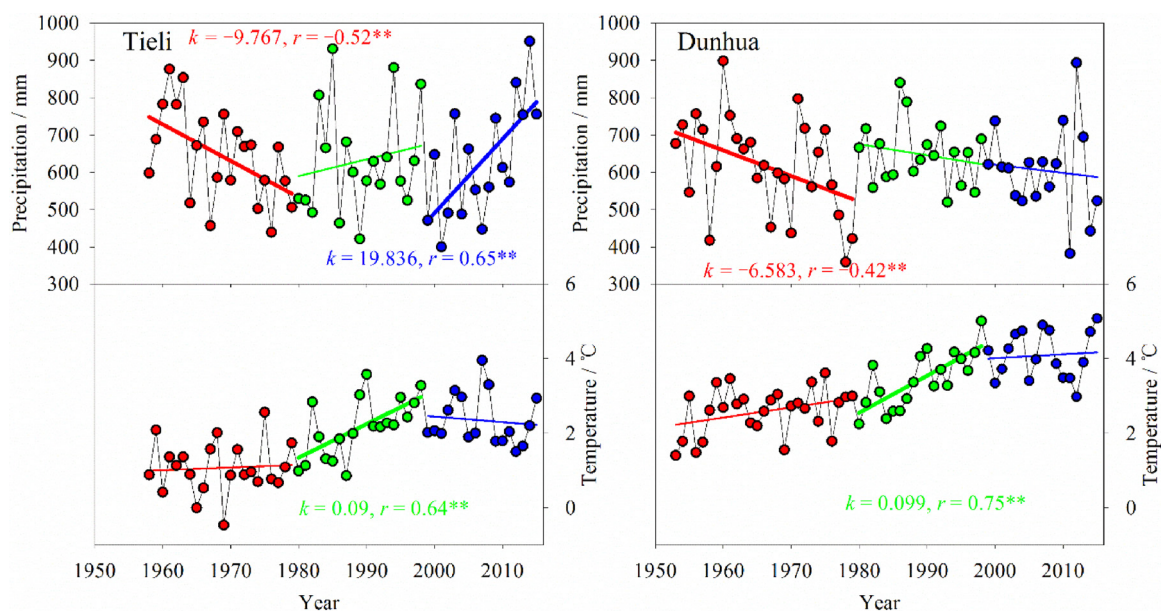


Fig. 4. The interannual variation of temperature and precipitation in Tieli and Dunhua weather station. The linear fittings are divided into three periods (before 1979, 1980–1998 and 1999–2015). The bold line indicates has a significant (**: $p < 0.01$) trend and the slope (k) and coefficient of determination (r) are highlighted on the figures.

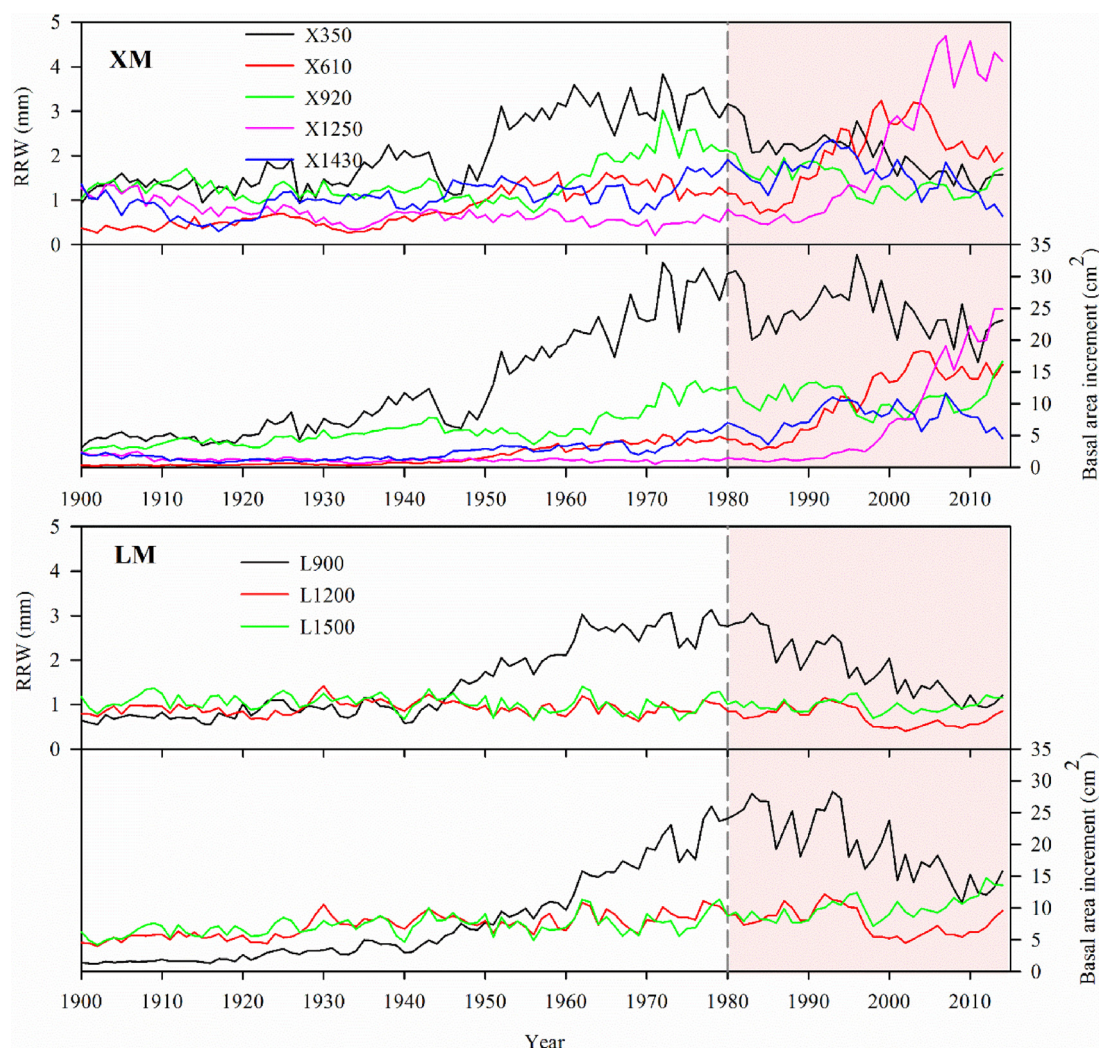


Fig. 5. Temporal variation of average basal area increment (BAI) and ring width (RRW) in XM and LM area.

the contrary, the positive effect of minimum temperature for all months except P12 was found in high-elevation trees (Fig. 7). Although the relationship between the maximum temperature and TRI was much weaker (only significant in months P9, C2, C6 and C9) than mean and minimum temperature, the opposite response to climate could also be found between low and high elevation. In short, a significant negative and positive effect of temperature on Yezo spruce growth occurred at low and high elevations, respectively (Fig. 7).

3.4. Changes in growth-climate relationship with time

Moving correlation analyses indicated a shift in dendroclimatic relations for precipitation and temperature with time, and a shift in growth-climate response was reversed in trees growing at low and high elevations (Figs. 8 and 9). The impact of precipitation in months P12 and C2 at low elevation sites shifted from positive before 1980 to negative after 1980. The impact of precipitation in month C1 and C3 shifted from non-significant negative before 1980 to significantly negative after 1980 (Fig. 8). On the contrary, the impact of precipitation

Table 4

Comparison of tree basal area increment (BAI) before and after 1980.

Site	Linear BAI trend 1947–1980			Linear BAI trend 1981–2014			Mean BAI (cm ²)	
	<i>k</i>	<i>R</i> _{adj}	<i>p</i>	<i>k</i>	<i>R</i> _{adj}	<i>p</i>	1947–1980	1981–2014
X350	0.634	0.915	< 0.0001	−0.137	0.367	0.0329	20.8 ± 6.92 a	24.28 ± 3.71 b
X 610	0.1	0.899	< 0.0001	0.468	0.9	< 0.0001	3.26 ± 1.1 a	10.77 ± 5.17 b
X 920	0.269	0.873	< 0.0001	−0.003	0.013	0.9413	7.87 ± 3.07 a	10.78 ± 2.16 b
X1250	−0.002	0.123	0.489	0.745	0.911	< 0.0001	1.11 ± 0.2 a	7.97 ± 8.15 b
X1430	0.083	0.662	< 0.0001	0.047	0.225	0.2017	3.6 ± 1.25 a	7.79 ± 2.07 b
L900	0.558	0.957	< 0.0001	−0.433	0.82	< 0.0001	14.63 ± 5.81 a	19.65 ± 5.26 b
L1200	0.069	0.483	0.0038	−0.101	0.473	0.0047	8.26 ± 1.43 a	7.78 ± 2.12 a
L1500	0.036	0.221	0.2097	0.122	0.643	< 0.0001	7.74 ± 1.61 a	9.98 ± 1.89 b

Note: *t*-test, the significantly (*p* < 0.05) difference between mean BAIs before and after 1980 are presented with different alphabets.

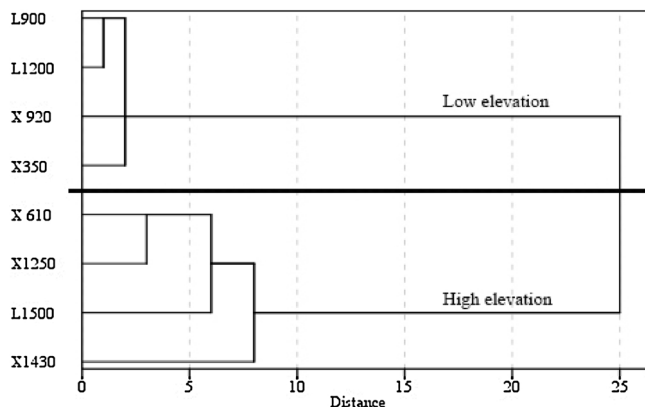


Fig. 6. Cluster diagram for tree growth and climate response (precipitation and mean temperature) of *Picea jezoensis* based on the complete linkage of correlation distances.

in C1–3 at high elevation shifted from non-significant before 1980 to significantly positive after 1980. The impact of precipitation in P12 was relatively stable with time as a significant positive correlation (Fig. 8).

Like precipitation, the impact of temperature at low elevations in months C5, C6 and C7 shifted from positive before 1980 to significantly negative after 1980. The impact of temperature in C9 and C10 shifted

from non-significant before 1980 to significantly negative after 1980 and the impact of temperature in C8 showed a significant negative correlation with time (Fig. 9). However, the impact of temperature at high elevation in months C7–C10 shifted from weak or non-significantly positive before 1980 to significantly positive after 1980, the impact of temperature in C5 and C6 shifted from significantly positive before the 1960s to non-significantly positive during the 1960s–1980s and then to significantly positive after the 1980s (Fig. 9).

A scatter plot of climate (temperature and precipitation) and averaged radial growth (TRI and BAI) of Yezo spruce indicated that the relationships between temperature/precipitation and TRI/BAI were different before and after 1980 (Fig. 10). At low elevations, the relationship between May–October temperature and TRI/BAI of Yezo spruce shifted from a non-significant increasing (pre-1980) to a significant decreasing trend (≥ 1980). However, at high elevations, the relationship between temperature and TRI/BAI shifted from a non-significant increasing trend (pre-1980) to a significant increasing trend (≥ 1980) (Fig. 10). Before and after 1980, the shift of the relationship between winter precipitation (December–March) and TRI/BAI at low and high elevations was consistent with the result of growing season temperature (Fig. 10).

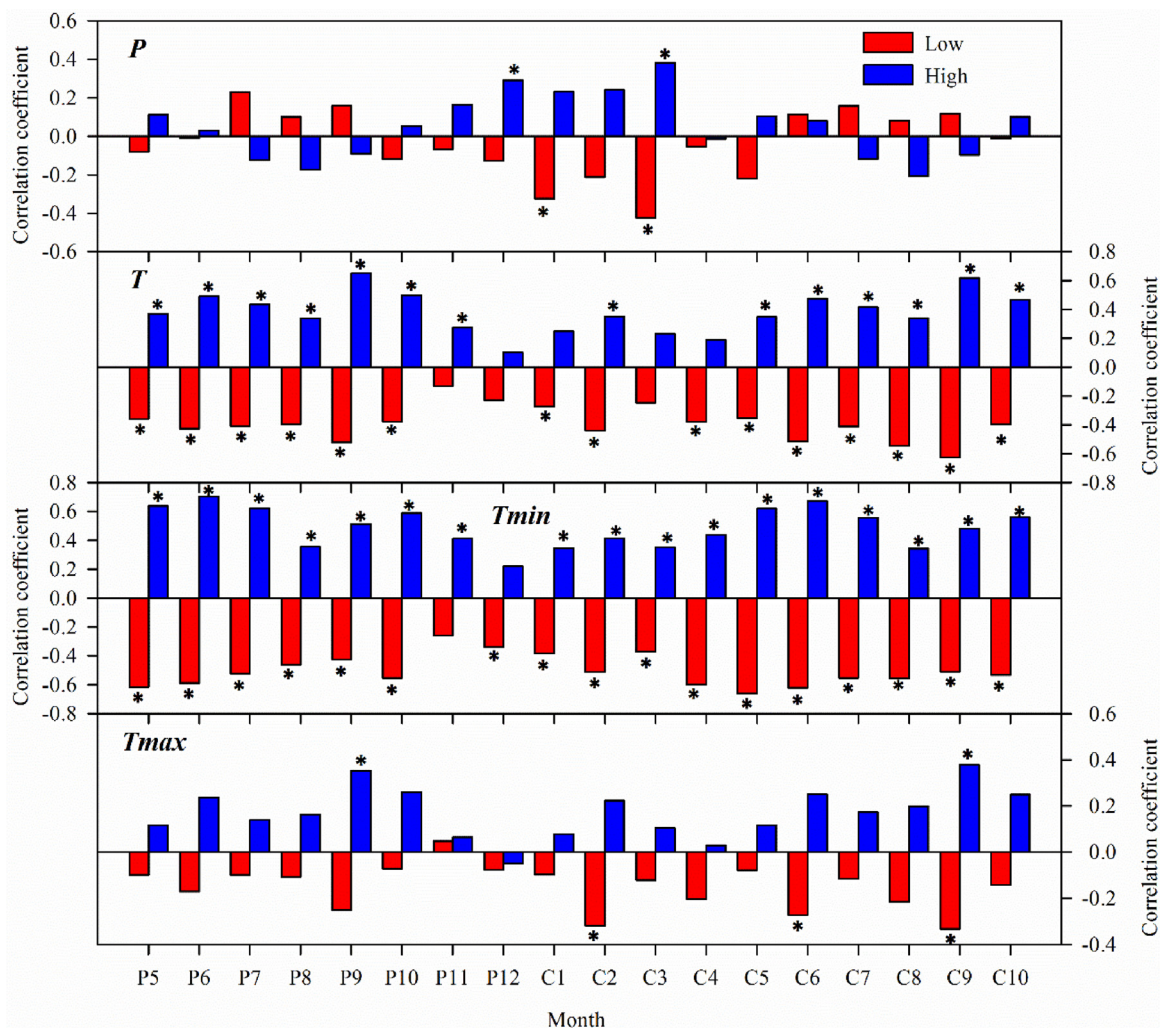


Fig. 7. Correlation coefficients between tree-ring chronologies at low and high elevations and regional monthly total precipitation, mean, minimum, and maximum temperature from previous May (P5) to current October (C10). Significant ($p < 0.05$) correlations are denoted by asterisks.

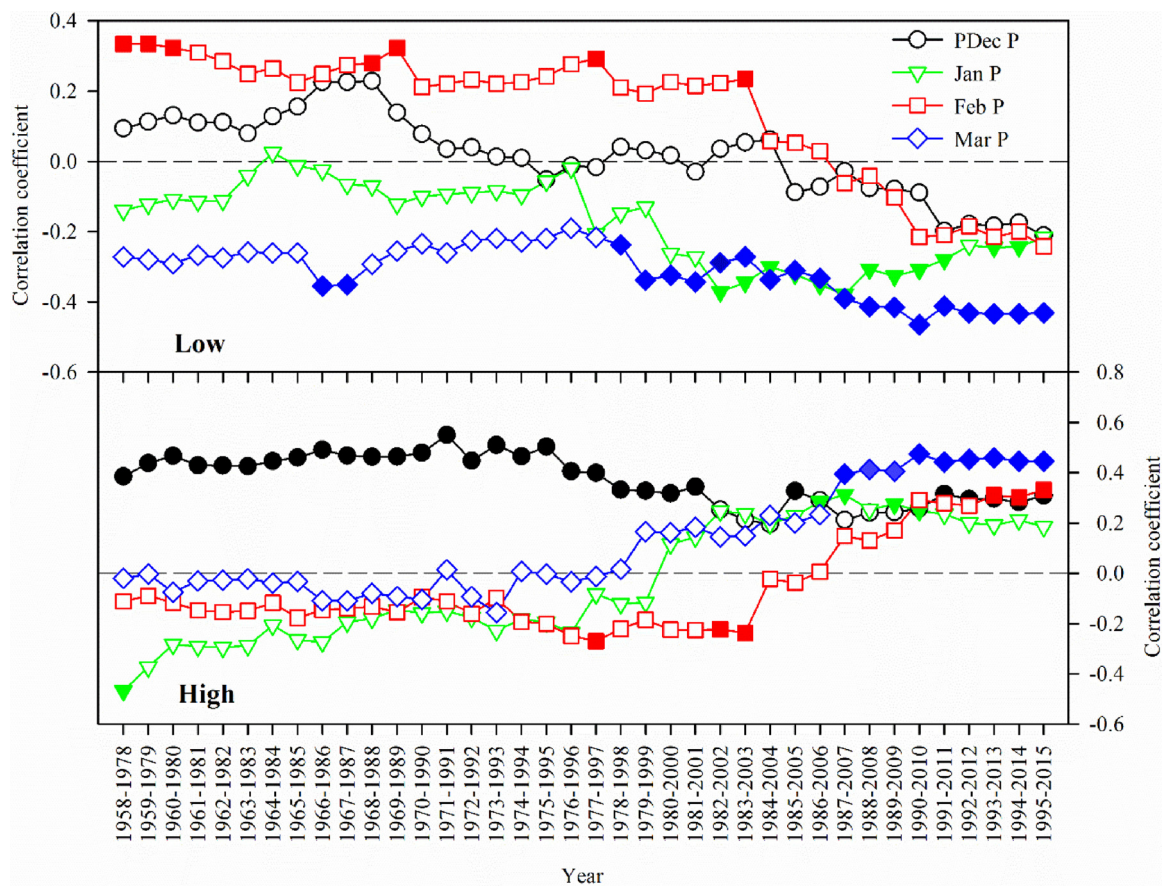


Fig. 8. Moving correlation function analysis with a 20-year window performed between the low- and high- elevation chronologies and the winter precipitation from December to March during the period 1957–2015. Significant ($p < 0.05$) correlations are present with color-filled.

4. Discussion

4.1. Recent contrasting growth with elevation

Rapid warming after 1980 increased the radial growth of Yezo spruce at high-elevation sites and decreased it at low-elevation sites. The contrasting tree growth along an elevation gradient has been demonstrated by previous studies (Salzer et al., 2009; Sidor et al., 2015). For example, in the White Mountains, California, USA, Salzer et al. (2009) found the radial growth of *Pinus longaeva* at low elevations showed a declining trend after the 1950s, while tree at high elevations had unprecedented increasing growth. However, in the Changbai Mountains, China, Yu et al. (2006) found that the growth of Yezo spruce decreased at all elevations (all non-significant) since the 1980s and more severe decline occurred at lower elevations due to the worse warming-related stress. It is likely that rising temperature at high-elevation shifted Yeddo spruce growth from negative to positive. According to the temperature of Dunhua weather station (to the south of LM) and the 0.6°C per 100 m of temperature difference along elevations, the annual mean temperature of site L1500 must be below -2.8°C . However, the annual mean temperature at the top site (ca. 1800 m) of Yeddo spruce in Changbai Mountains is -2.8°C (Yu et al., 2006), which is close to the temperature at 1200–1500 m sites of LM. Therefore, the slight declining of Yeddo spruce at high elevations of Changbai Mountains after 1980 is reasonable.

Trees at low elevation showed a rapid decrease of ring widths after warming (1980), which is consistent with the variation of temperature anomalies in China (Tang and Ren, 2005). The gradual reduction of water stress with the decrease of mean annual surface air temperature during the 1940s–1980s (from positive to negative) is correlated with

the increase of ring widths, while the rapid warming after the 1980s was accompanied by the increase of water stress forming narrow rings (Tang and Ren, 2005). After warming, the positive effects of temperature on trees growth at low elevations are decreasing and the negative effects are more and more critical (Fritts, 1976; Barber et al., 2000; Sidor et al., 2015). This warming-induced drought stress during the 20th century has been found in White spruce (*Picea glauca*), Norway spruce (*Picea abies*), Korean spruce (*Picea koraiensis*), Korean pine (*Pinus koraiensis*), and Hinggan fir (*Abies nephrolepis*) (Barber et al., 2000; Li et al., 2011; Yao, 2013; Sidor et al., 2015; Wang et al., 2016). Wang et al. (unpublished) found that the rapid warming was an important factor in the growth decline of Korean pine in NE China after the 1980s. However, trees growing at high elevations shifted from slow and stable growth to rapid increase growth after 1980, which indicated that temperature played a positive effect on growth (Fritts, 1976; Jump et al., 2006; Yu et al., 2006; Sidor et al., 2015). The warming could also prolong the length of growing season at high elevations, which may accelerate tree growth at high elevations after 1980 (Fritts, 1976; Hallinger et al., 2010; Sidor et al., 2015). This accelerating growth of trees at high-elevation sites after warming was consistent with previous evidences at alpine treeline (Gou et al., 2007; Salzer et al., 2009; Millar et al., 2015). For example, Millar et al. (2015) found that the growth patterns of pines (*Pinus flexilis* and *Pinus longaeva*) at the upper treeline showed an episodic increase in growth after 1963 in the western Great Basin, USA. These physiological explanations in the contrasting growth of Yeddo spruce along an elevation gradient was further confirmed by our moving correlation function analysis.

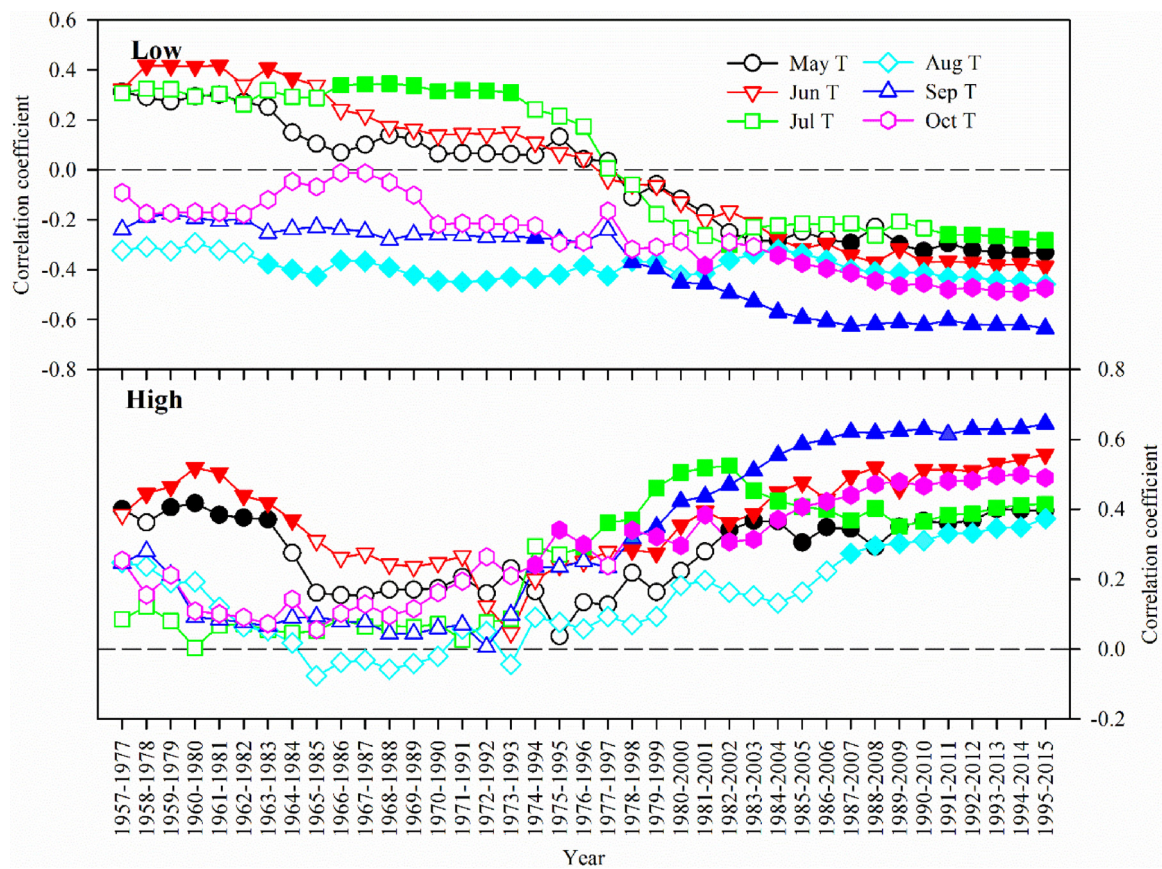


Fig. 9. Moving correlation function analysis with a 20-year window performed between the low- and high- elevation chronologies and the current temperature from May to October during the period 1957–2015. Significant ($p < 0.05$) correlations are present with color-filled.

4.2. Dendroclimatic relationships and its shifting around 1980

The growth-climate relationships of Yezo spruce at low-elevation sites were remarkably inverse of that at high elevations, especially for the growing season (May–October) temperature. Temperature is a major limiting factor of radial growth in several spruce species in the world, such as White spruce (Barber et al., 2000), Norway spruce (Sidor et al., 2015), Yeddo spruce (Yu et al., 2006) and Korean spruce (Yao, 2013). In this study, a significant positive and negative effect of growing season temperature on the radial growth of Yezo spruce were found at high- and low-elevation sites, respectively. This different effects of growing season temperatures on radial growth of Norway spruce at high (> 1300 m a.s.l.) and low (< 1000 m a.s.l.) elevations was also found in the eastern Carpathians of Romania (Sidor et al., 2015). Recent warming significantly prolongs the length of growing season and results in wide rings at high elevation (Fritts, 1976; Sidor et al., 2015). At warmer low-elevation sites, however, drought stress due to warming related high evapotranspiration rates reduces carbohydrate synthesis and then results in a narrow ring (Fritts, 1976). The negative effect of warming-included drought on tree growth might be more serious than the positive effect caused by warming at low-elevation sites (Yu et al., 2006; Wang et al., 2016). Therefore, soil water deficits caused by thermal stress of higher temperature is usually the critical factor that limiting tree growth at lower elevations. Previous studies in surrounding areas had found the warming-related drought caused the growth decline of Korean pine, Korean spruce and Hinggan fir at low elevations (< 900 m) (Yao, 2013; Wang et al., 2016). Climatic factors limiting tree growth along elevational gradient were typically moved from water shortage at low elevations to low-temperature limitation at higher elevations, which has been found in temperate and boreal forests (Yu et al., 2006; Babst et al., 2013). In Changbai

Mountains, Yu et al. (2006) found the Yezo spruce was more affected by precipitation at the lower limit of its distribution and more affected by temperature at the upper limit of its distribution, which further confirmed our results.

Moreover, winter temperatures and precipitation could also be the limiting factors of Yezo spruce radial growth, and their impacts on the radial growth of Yezo spruce were also inverse at low- (negative) and high-elevation (positive) sites. Higher winter temperatures not only can favor tree growth in the coming year by protecting rooting system to uptake water mineral nutrient, increasing the photosynthesis rate and reducing the occurrence of frost disaster; but also can decrease tree growth in the coming year by promoting the water evaporation and snow melt related drought/water stress during the growing season and increasing the respiration rate, etc. (Yu et al., 2006; Jørgen et al., 2015; Sidor et al., 2015; Zhu et al., 2015a). For instance, the dynamics and activities of fine roots are important to uptake water and mineral nutrient. However, a big consumer of carbohydrates (approx. 30% of the global net primary production) (Jackson et al., 1997) may be influenced by winter temperature-included soil-frost events. More winter precipitation at low-elevation sites may delay the onset of cambial activity, which results in a shorter growing season (Fritts, 1976; Pellizzari et al., 2014). At high-elevation sites, a deeper snow accumulation may insulate the ground creating warmer soils that may decrease possible frost damage, promote microbial activity and increase nutrient supply (Hallinger et al., 2010; Jørgen et al., 2015).

The dendroclimatic relations of Yezo spruce showed a distinct shift around 1980, which might be related to recent rapid warming coupled with a slight decrease in precipitation. Similar patterns were also found in nearby dendroclimatic studies (Li et al., 2011; Zhu et al., 2015b). For instance, Zhu et al. (2015b) found a clear shifting in dendroclimatic relationships between the TRI of Korean pine and Hinggan fir and

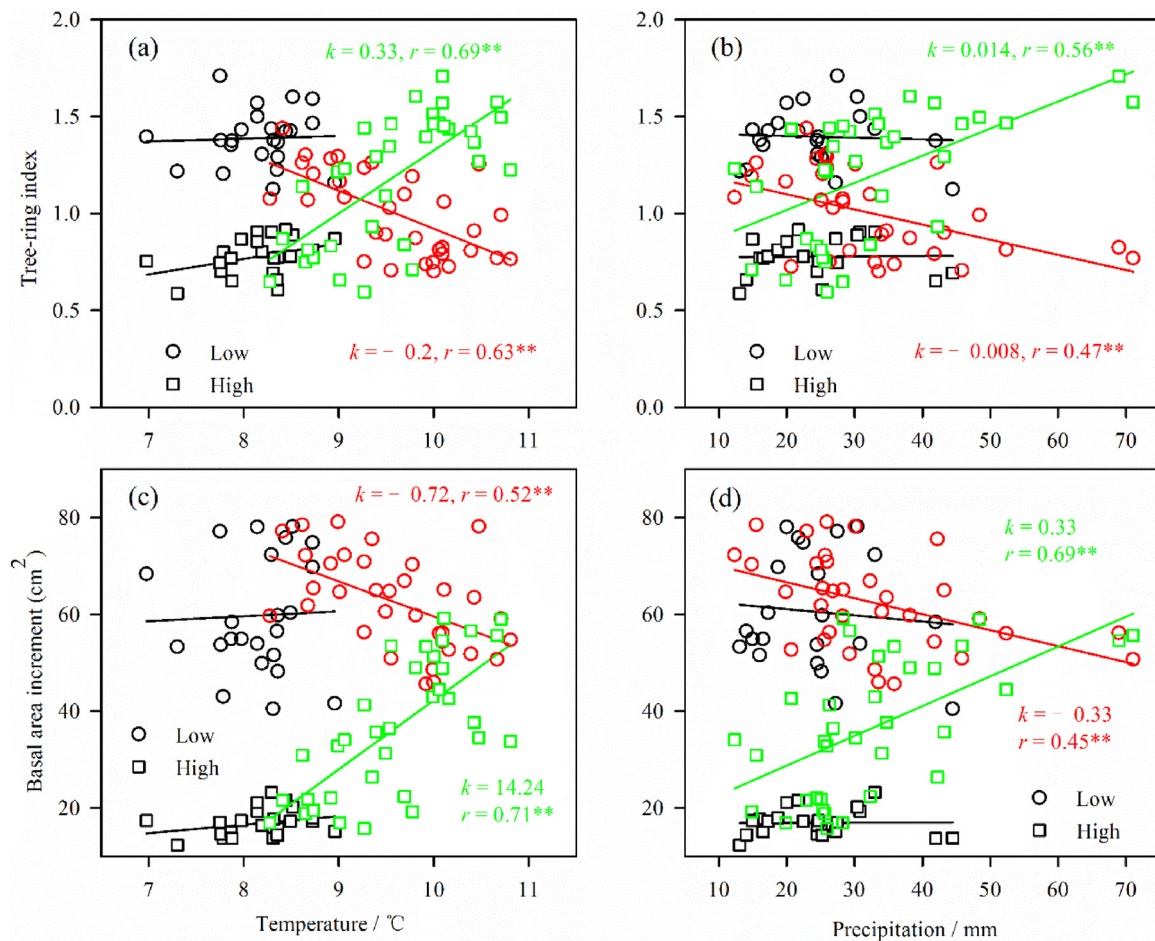


Fig. 10. Scatter plot between climate (May–October temperature and December–March precipitation) and averaged radial growth (TRI and BAI) at low and high elevations. The black and color circles/squares represent the value before and after 1980, respectively. The slope (k) and correlation coefficient (r) of significant linear regressions were highlight in figure.

climate around 1980. At low elevations, the rapid warming-included water loss/evapotranspiration coupled with the decline of precipitation may cause severe drought stress after 1980. The water availability decline or drought stress leads to the positive effect of temperature on radial growth of Yezo spruce shifting into the negative effect. However, precipitation generally increases with elevation increase, and water/drought stress usually decrease (Yu et al., 2006). Consequently, the negative effect of rapid warming on the radial growth of Yezo spruce shifted into positive when the temperature/elevation exceeds a certain threshold (Salzer et al., 2009; Sidor et al., 2015). At high elevation sites, higher temperature usually accompanied by longer growing season, which cause a shifting from negative to positive in tree growth-climate relationships after warming. Moreover, the shifting from positive (negative) to negative (positive) of winter (P12–C3) precipitation also occurred at low- and high-elevation sites after warming. Before 1980, more winter precipitation/snow may provide more water for the radial growth of Yezo spruce at the beginning of growing season at low-elevation sites, while it indirectly shortened the length of growing season at high-elevation sites (Fritts, 1976). After 1980, however, higher temperature at low elevations may cause earlier snow melt and increase evapotranspiration, which indirectly caused drought stress at the beginning of growing season (Fritts, 1976; Pellizzari et al., 2014). At high-elevation sites, the negative effects of strong snowfall were offset by high temperatures and at the same time it brings more water for the radial growth of Yezo spruce at the beginning of growing season (Yu et al., 2006; Sidor et al., 2015).

4.3. Implications for forest management under climate change

Many studies on climate change have been carried out in the world forests, but few studies have focused on its impact along an elevation gradient (Sidor et al., 2015). Our key finding is that climate warming, especially since 1980, significantly reduced Yezo spruce growth at low elevation sites and conversely induced a rapid growth increase at high elevation sites. It highlights that the elevation-related growth response to climate must be considered in managing forests, forecasting forest dynamics, as well as estimating forest productivity or carbon storage under future climate change. If climate warming continues or intensifies, Yezo spruce at low elevations may decline or die, while Yezo spruce at high elevations may accelerate growth or prevail based on our results. The spruce forests in our study areas could be a huge potential carbon sink at high elevation and carbon source at low elevation. In addition, it is important to consider and use this change to regulate forest carbon emissions. However, in some vulnerable sites where trees have shown a remarkable decline, the nurturing measures to alleviate the high risk of tree death caused by climate change are needed, and forest harvesting should be given priority at these sites to maximize resource utilization. Moreover, the afforestation of Yezo spruce should be given priority at high elevations. In fact, the negative effects of climate change on forests in NE China might be more serious than the positive ones, since most Yezo spruces dominate low elevations (Zhou et al., 2002). Furthermore, other negative effects may be accompanied by forest decline, for example, plant diseases, insect pests, and forest fires as well as changes in forest structure and function that could lead

to a faster decline of tree vigor. Previous studies have confirmed that forest decline were more vulnerable to the outbreaks of bark beetle (Bentz et al., 2009) and forest fire (Miller et al., 2009) in western North America.

We do not anticipate a complete change in growth across Yezo spruce's range only based on elevation because many biotic and abiotic factors, which should be considered in forest practice, can also influence tree growth and the interactions between forest ecosystems and climate. Microclimate created by site conditions, such as soil substrate and ground cover, can also influence tree growth. For instance, at the soils-boulders mixed X920 (mid-high elevation) site, trees have a similar growth pattern and dendroclimatic relationship with trees in X350 site (low elevation). Species competition could also make tree growth a tremendous change (Cook, 1985; Fritts, 1976; Orwig and Abrams, 1997). The difference of competition rates in hardwood forest (stronger interspecific competition) and sub-alpine forests (stronger intraspecific competition) might influence tree growth of Yezo spruce. For example, any endogenous changes in intraspecific competition occurred in low-elevation hardwood forests could dramatically affect the competition rates, which might change Yezo spruce growth in hardwood forest compared to sub-alpine forests. In addition, the latitude-related effect of climate warming on tree growth, i.e. climate warming might exacerbate the negative effects of temperature or drought on tree growth at low latitude, but benefit tree growth at high latitude (Huang et al., 2010; Mäkinen et al., 2002). In this study, the two sample sites show a 1.4 °C difference, rapid warming might more negatively affect tree growth at low latitude than that at high latitude. To predict the radial growth changes of Yezo spruce throughout its whole distribution area under future warming scenario, the latitude difference should be considered.

Unfortunately, we couldn't estimate the temperature/elevation threshold that separate the positive and negative effects of climate change on tree growth due to the limitation of sampling sites and the elevation gradient. Other major conifers including Korean pine, Korean spruce and Hinggan fir have also suffered a decline in parts of NE China during recent decades (Li et al., 2011; Yao, 2013; Wang et al., 2016). Whether they show different growth patterns with elevation needs additional study, which is important for forest management and practice.

5. Conclusions

A significantly wider mean ring width and higher BAI of Yezo spruce were found at low elevation than high elevation. Both ring width and BAI of Yezo spruce at low-elevation sites showed a clear increase during 1940s–1970s and a significant decline from 1980 to present, while trees at high elevations showed an accelerated increase in ring width and BAI trend until the end of 1980s. Rapid warming after 1980 increased the radial growth of Yezo spruce at high elevation and decreased tree growth at low elevation. Winter precipitation and growing season temperature have a significant positive/negative effect on Yezo spruce radial growth at high-/low-elevation sites. In addition, the effect of winter precipitation and growing season temperature on tree growth at low elevations shifted from positive to negative before and after 1980, while it shifted from negative to positive at high elevation sites. Microclimate caused by substrate and ground cover may lead to the effect of climate changes on tree/forest growth from positive to negative. The difference in water stress caused by rapid warming is likely a prominent factor resulting in the elevation-related contrasting growth or response of Yezo spruce in NE China. Our findings suggest that the elevation-related growth response to climate warming should be integrated into the prediction model of estimating the possible patterns of future carbon cycles and forest dynamics. Whether this elevation-related response of tree growth to warming occurs in other tree species in NE Asia needs further study.

Acknowledgements

This work was supported by the National Key Research and Development Program of China (2016YFA0600800); the National Natural Science Foundation of China (41471168); the Program for New Century Excellent Talents in University (NCET-12-0810); and the Program for Changjiang Scholars and Innovative Research Team in University (IRT-15R09). We thank the staff of the sampled Forestry Bureaus for their assistance in the field.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.dendro.2018.05.002>.

References

- Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanic, T., 2013. Site- and species-specific responses of forest growth to climate across the European continent. *Glob. Ecol. Biogeogr.* 22, 706–717.
- Barber, V.A., Juday, G.P., Finney, B.P., 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405, 668–673.
- Bentz, B., Logan, J., MacMahon, J., Allen, C.D., Ayres, M., Berg, E., Carroll, A., Hansen, M., Hicke, J., Joyce, L., 2009. Bark Beetle Outbreaks in Western North America: Causes and Consequences. Blackwell Publishing Ltd.
- Biondi, F., Waikul, K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput. Geosci.* 30, 303–311.
- Camarero, J.J., García-Ruiz, J.M., Sangüesabarreda, G., Galván, J.D., Alla, A.Q., Sanjuán, Y., Beguería, S., Gutiérrez, E., 2015. Recent and intense dynamics in a formerly static Pyrenean treeline. *Arct. Antarct. Alp. Res.* 47, 773–783.
- Consortium, P.K., 2013. Continental-scale temperature variability during the past two millennia. *Nat. Geosci.* 6, 339–346.
- Cook, E.R., 1985. A Time Series Analysis Approach to Tree Ring Standardization. University of Arizona, Arizona, USA.
- Dai, A., 2013. Increasing drought under global warming in observations and models. *Nat. Clim. Change* 3, 52–58.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Elsevier, Amsterdam, Netherlands.
- Gou, X., Chen, F., Jacoby, G., Cook, E., Yang, M., Peng, J., Zhang, Y., 2007. Rapid tree growth with respect to the last 400 years in response to climate warming, north-eastern Tibetan Plateau. *Int. J. Climatol.* 27, 1497–1503.
- Hallinger, M., Manthey, M., Wilmking, M., 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytol.* 186, 890–899.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* 43, 69–78.
- Huang, J., Tardif, J.C., Bergeron, Y., Denneler, B., Berninger, F., Girardin, M.P., 2010. Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Glob. Change Biol.* 16, 711–731.
- IPCC, 2013. *Climate Change 2013: the Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge.
- Jørgen, H., Agata, B., Grzegorz, R., Hansen, B.U., Hansen, M.O., Ole, S., Bo, E., 2015. Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. *Glob. Change Biol.* 21, 2410–2423.
- Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci. U. S. A.* 94, 7362–7366.
- Jump, A.S., Hunt, J.M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob. Change Biol.* 12, 2163–2174.
- Li, G., Bai, F., Sang, W., 2011. Different responses of radial growth to climate warming in *Pinus koraiensis* and *Picea jezoensis* var. *komarovii* at their upper elevational limits in Changbai Mountain, China. *Chin. J. Plant Ecol.* 35, 500–511.
- Li, J., 1997. *Korean Pine Mixed Forest Ecology and Management*. Northeast Forestry University Press, Harbin.
- Liu, H., Williams, A.P., Allen, C.D., Guo, D., Wu, X., Anenkhonov, O.A., Liang, E., Sandanov, D.V., Yin, Y., Qi, Z., 2013. Rapid warming accelerates tree growth decline in semi-arid forests of Inner Asia. *Glob. Change Biol.* 19, 2500–2510.
- Mäkinen, H., Nöjd, P., Kahle, H.P., Neumann, U., Tveite, B., Mielikäinen, K., Röhle, H., Spiecker, H., 2002. Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. *For. Ecol. Manage.* 171, 243–259.
- Millar, C.I., Westfall, R.D., Delany, D.L., Flint, A.L., Flint, L.E., 2015. Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883–2013), in the western Great Basin, USA. *Can. J. For. Res.* 45, 1299–1312.
- Miller, J.D., Safford, H., Crimmins, M., Thode, A., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12, 16–32.
- Orwig, D.A., Abrams, M.D., 1997. Variation in radial growth responses to drought among species, site, and canopy strata. *Trees* 11, 474–484.

- Pellizzari, E., Pividori, M., Carrer, M., 2014. Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps. *Environ. Res. Lett.* 9, 104021.
- Phipps, R.L., John, C.W., 1998. Decline in long-term growth trends of white oak. *Can. J. For. Res.* 18, 24–32.
- Salzer, M.W., Hughes, M.K., Bunn, A.G., Kipfmüller, K.F., 2009. Recent unprecedented tree-ring growth in Bristlecone pine at the highest elevations and possible causes. *Proc. Natl. Acad. Sci. U. S. A.* 106, 20348–20353.
- Sidor, C.G., Popa, I., Vlad, R., Cherubini, P., 2015. Different tree-ring responses of Norway spruce to air temperature across an altitudinal gradient in the Eastern Carpathians (Romania). *Trees* 29, 985–997.
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-Ring Dating*. University of Arizona Press, Arizona, USA.
- Tang, G., Ren, G., 2005. Reanalysis of surface air temperature change of the last 100 years over China. *Clim. Environ. Res.* 10, 791–798.
- Thomas, P., Zhang, D., Katsuki, T., Rushforth, K., 2013. *Picea jezoensis*. The IUCN Red List of Threatened Species 2013: e.T42325A2665. Downloaded on 22 March 2017. <https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T42325A2665.en>.
- Wang, X., 2015. *Dendroecological Studies of Dominant Tree Species along an Altitudinal Gradient on Changbai Mountain, Northeastern China*. PhD Thesis. Beijing Forestry University, Beijing.
- Wang, X., Zhang, M., Ji, Y., Li, Z., Li, M., Zhang, Y., 2016. Temperature signals in tree-ring width and divergent growth of Korean pine response to recent climate warming in northeast Asia. *Trees* 31, 415–427.
- Yao, Q., 2013. *Climate-growth Relationships of Spruce-fir and Their Connection With Large-Scale Climate Change in Xiaoxing'an Mountains, China*. Master's Thesis. Northeast Forestry University, Harbin.
- Yu, D., Wang, Q., Wang, G.G., Dai, L., 2006. Dendroclimatic response of *Picea jezoensis* along an altitudinal gradient in Changbai Mountains. *Sci. China Ser. E: Technol. Sci.* 49, 150–159.
- Zhou, G., Wang, Y., Jiang, Y., 2002. Global change and water-driven IGBP-NECT, Northeast China. *Earth Sci. Front.* 9, 198–216.
- Zhu, L., Li, S., Wang, X., 2015a. Tree-ring reconstruction of February–March mean minimum temperature back to 1790A.D. Yichun, Northeast China. *Quat. Sci.* 35, 1175–1184. <http://dx.doi.org/10.11928/j.issn.1001-7410.2015.05.13>.
- Zhu, L., Yang, J., Zhu, C., Wang, X., 2015b. Influences of gap disturbance and warming on radial growth of *Pinus koraiensis* and *Abies nephrolepis* in Xiaoxing'an Mountain, Northeast China. *Chin. J. Ecol.* 34, 2085–2095.